"In the few specimens of *Amauris echeria* that I tried I found that no juice was emitted, but they had a nauseous taste and a strong smell, which reminded me somewhat of that emitted by many *Coccinellidæ*. But it was *L. chrysippus* which showed me the futility of trying to arrive at any definite conclusions from this line of research, for it emits neither juice nor smell, and I could detect no trace of any taste, unpalatable or otherwise, but the tissues have a somewhat soapy feel to the tongue, which I noticed in *A. echeria* and some of the Acræas. The same may be said of *Mylothris agathina*, though from its conspicuous colouring, slow flight, and wide dispersal, I feel sure it is an inedible species.

"*Malvern, Feb.* 21, 1897.—*Acræa horta* exudes a bitter yellow juice from the thorax when it is injured, and this juice permeates the costa of the fore-wing. The head and abdomen do not appear to me to have any unpleasant taste. Trimen refers to their smell, but my smelling powers are not sufficiently acute to detect it.

"*Malvern, May* 14, 1897.—*Alæna amazoula* feigns death most persistently; it has an unpleasant taste and strong smell not unlike that of the *Coccinellidæ*."

28. Guy A. K. Marshall's Proof of Seasonal Changes in South African Butterflies of the Genus *Precis*. (E. B. P.)

A. *Introduction.*

The attempt will be made in the following section of this memoir to explain these astonishing changes as due to the adaptation of a moderately distasteful and protected genus in two directions—towards conspicuous warning colours in the generations of the wet season, the time when insect-food is abundant; towards procryptic concealment in the pressure and scarcity of the dry season.

Facts which require for their interpretation the hypothesis of adaptation in the direction of conspicuousness will be brought forward, much use being made of the conclusive proof only recently obtained by Mr. Marshall, by breeding the one from the other, that *Precis simia* is the wet phase of *P. antilope*.

The distinct habits and stations of the two phases, their relation to other seasonal forms of butterflies, the observed

differences in the insect life of the two seasons, will all be shown to be consistent with the above hypothesis.

The results of Mr. Marshall's experiments as to the nature of the stimulus by which the change is started in any individual will be discussed, and further lines of investigation suggested. The much greater size and weight of the dry phases will be shown to have an important bearing upon the inquiry, indicating, as it does, that the phase must be predetermined in the larval stage.

Finally, it will be argued that the facts proved by Mr. Marshall, although most startling and indeed astounding, are not subversive of any of the principles of the science of systematics.

B. *Historical.*

In his great work on "South African Butterflies" (London, 1887, vol. i), Mr. Roland Trimen describes several intermediate varieties between *Precis natalensis* and *P. sesamus*, and records Mr. F. N. Streatfeild's capture of the two butterflies *in coitu*. He concludes (*loc. cit.* pp. 231 and 233), "It is only to such occasional unions, and to their fertility, that the origin of the intermediate examples under notice can be attributed."

Mr. Trimen also makes a similar suggestion as to the intermediate varieties between *pelasgis* and *archesia*, which are also recorded as having been taken *in coitu* (*loc. cit.* p. 235).

Mr. Guy A. K. Marshall first published in 1896 the suggestion that a group of South African butterflies described and known as different species of the genus *Precis* or *Junonia* were in reality the seasonal phases of a comparatively limited number of species. He pointed out, however, that *octavia* and *amestris* (*s. l.*) had been previously considered as two forms of a single species by M. Charles Oberthür of Rennes (Ann. Mus. Genov. xviii, 1883, p. 721), and also that Mr. C. N. Barker, the distinguished Natal naturalist, had been long convinced of the existence of these seasonal phases, and especially of the most remarkable case of all, *P. sesamus*, and its wet-season form, *natalensis*.

Mr. Marshall's general description of the differences between the two phases is as follows: "The dry-season form is smaller, and usually assumes a duller type of colouring on the upper-side, sometimes of quite a different hue; the

under-side becomes of a general brownish tint, more or less resembling a withered leaf, the likeness being heightened by an oblique line running from the apex of fore-wing to the anal angle of hind-wing, representing the mid-rib; also by the marked prolongation of the fore-wing, so well known in the winter form of *Melanitis leda*. Lastly, the ocelli on the under-side are much reduced or obsolescent" (Trans. Ent. Soc. Lond., 1896, p. 557). I am unable to understand the opening statement that "the dry-season form is smaller," indeed, Mr. Marshall criticizes a more general statement of the same kind made by Mr. C. N. Barker (*loc. cit.* p. 551). In the very first species described from this point of view by Mr. Marshall, *Precis tugela*, he speaks of "the smaller summer form," and the only other *Precis* in which he speaks of a difference in size is *P. artaxia*, of which he uses almost the same words (p. 561). I have since compared the two phases of the following species in the Hope Collection, with results shown below:—

Precis tugela, dry phase larger.
„ *ecryne*, „ „ much larger.
„ *actia*, „ „ „ „
„ *pelasgis*, „ „ rather „
„ *sesamus*, „ „ distinctly larger.*
„ *antilope*, „ „ much „
„ *artaxia*, „ „ „ „

See also pages 451 and 456 for the proof by weighing of the great difference between some of these phases.

Since the above paragraph was written Mr. Marshall has informed me that the statement was certainly a slip of the pen, which remained uncorrected, because he was unfortunately unable to see the proofs of his paper.

Although Mr. Marshall anticipated the results of future discovery in a truly remarkable manner in this memoir (Trans. Ent. Soc. Lond., 1896, p. 557), and brought forward evidence of a most convincing kind, yet the conclusion which required to be proved was to most naturalists so highly improbable, because of the extraordinary differences between the supposed species, that nothing less than the actual breeding of one form from another was sufficient.

In his second paper on the subject (Ann. and Mag. Nat.

* Difference much less marked in specimens from northern part of range.

Hist., ser. 7, vol. ii, July 1898, p. 30), which it is only just to describe as epoch-making in the history of seasonal dimorphism, Mr. Marshall recorded this great discovery, and published the fact that he had succeeded in breeding *sesamus* from *natalensis* in three cases. The specimens themselves Mr. Marshall presented in two cases to the Hope Collection at Oxford, in the third to the British Museum of Natural History. The Oxford specimens are figured on Plate XII, figs. 1 and 2 the parents, figs. 1*a*, 1*b*, and 2*a* the offspring. The dates of the various stages are given in the description of the plate.

These specimens must always have historic interest, and I have therefore published in the plates accompanying this memoir a representation of the whole of the evidence obtained by Mr. Marshall in 1898, so far as it is at my disposal. The extracts from Mr. Marshall's letters bearing on the same subject have also historic interest, and are therefore recorded in full below.

"*Umkomaas Mouth, Natal; Sept.* 3, 1897.—I am sorry to say I have never yet bred *natalensis* through to *sesamus*. At Karkloof, Natal, I managed to secure three eggs in March (just the right month for the purpose of testing the hypothesis that they are the same species), and one of the resulting larvæ was fully half-grown when I left there for Malvern, near Durban. I brought them down with me, as I knew that C. N. Barker had bred *natalensis* from the larva, and so would know their local food-plant. The Karkloof plant does not occur at Malvern, and the larvæ utterly refused the Malvern food-plant and everything else I tried them with; so they pined away and died.

"I have not the least doubt of the specific identity of these two forms; they are undoubtedly confined respectively to the wet and dry seasons, they have been frequently observed *in coitu*, and intermediate forms occur at the change of seasons. The larvæ are identical and feed on the same plant; for out of twelve larvæ taken by Hutchinson off one plant, ten were *natalensis* and two *sesamus*. I always think *natalensis* is an interesting species as showing the brilliant colours which can be acquired by an unprotected species without detriment. A newly-emerged *natalensis* is a glorious insect, and rivals the brightest Acræas in its colouring on both surfaces; moreover, it is a frequenter of open country, where its salmon-red wings

are a conspicuous object as it sits sunning itself on plants or stones. But it is very wary and difficult of approach, being kept on the alert by its enemies, the lizards. I have often watched these little reptiles stalking both *natalensis* and *pelasgis* round the stones, and have seen them capture and eat both species."

"*Salisbury, March* 6, 1898.—You will be pleased to learn that within another few weeks I hope to have been able to have solved the *natalensis-sesamus* question. Three weeks ago I obtained five eggs from a female of typical *natalensis;* two proved infertile, one young larva I lost, but the remaining two are thriving and growing splendidly. Later on I got three more eggs, which have hatched successfully. To-day I took one more, and also, which pleased me much, an egg of typical *Precis simia*, which I am convinced is the wet-season form of *P. cuama* (Hew.), in spite of Butler's remarks. The *natalensis* question I am all the more anxious to settle, as I have now strong collector's evidence against me, viz. Distant, who records that he only took one *natalensis* at Pretoria, whereas *sesamus* was abundant and occurred all through the wet season."

"*Salisbury, June* 5, 1898.—You will be glad to learn that I have at last proved the identity of *P. sesamus* and *natalensis* by breeding the former from eggs laid by the latter in three instances, and I send you the parent and offspring in two of the cases, the third I am sending to the British Museum. You may imagine my delight on seeing the first specimen emerge, for though I felt convinced that the result would be as I anticipated, yet Distant's remarks raised a haunting fear that perhaps I had made a big mistake after all. However, I am glad to say this was not so."

C. *The Demonstration by* Guy A. K. Marshall *that* Precis simia *is the Wet Phase of* P. antilope.

Only a few weeks ago Mr. Marshall obtained this further proof of the soundness of the conclusions he reached, and the validity of the evidence he adduced in 1896. A female specimen of *P. simia* was tracked while she laid nine eggs, on Feb. 23, 1902, at Salisbury. The butterfly was then captured, and is represented on Plate XII, fig. 3, and the under-side on Plate XIII, fig. 4. Offspring of

the form *antilope* were successfully reared from two of these eggs. In the case of the first, shown on Plate XII, fig. 3*a* (under-side on Plate XIII, fig. 4*a*), the egg hatched on March 1, the larva pupated on April 10, and the imago, a female, emerged on April 27. In the case of the second, shown on Plate XII, fig. 3*b* (under-side on Plate XIII, fig. 4*b*), the egg hatched on March 1, the larva pupated on April 14, and the imago, a male, emerged on April 29. All three specimens have been presented by Mr. Marshall to the Hope Collection at Oxford. The great difference between the under-sides of the two offspring (compare Fig. 4*a* with 4*b* on Plate XIII) is deeply interesting. Although so widely different, both equally resemble dead leaves, recalling the various distinct forms of dead leaf represented by the under-sides of the individuals of the same species of *Kallima*. The difference between the outline of the wings in parent and offspring is seen to be far greater in this species than in *sesamus* and *natalensis*, and *archesia* and *pelasgis*, as will be at once seen when the figures on Plate XII or Plate XIII are compared.

Mr. Marshall's account of his success in obtaining the material by which he proved the identity of *antilope* and *simia*, was received in the following paragraph of one of his letters.

"*Salisbury, Feb.* 26, 1902.—I cannot even now agree with Butler's arrangement of *Precis antilope* and *cuama*. For although their extreme forms appear to be very distinct, yet all the chief distinctive characters are unstable and tend to converge. Aurivillius agrees with me in regarding them as conspecific, though he separates *trimeni* and *simia*. A pair of these latter I took *in copulâ* last season, which is sufficient evidence as to their identity in my mind, for I am very sceptical as to interbreeding in a case such as this. However, I have determined to solve the problem this season, and since my return most of my time out-of-doors has been spent in trying to secure authenticated eggs of either summer form. Last Sunday I succeeded at last! I got nine eggs from a single *simia*, and they will probably hatch to-morrow; I hope I shall succeed in pulling most of them through. All my larvæ died in the first stage last year, for owing to the erratic way in which the females lay I could not ascertain the true food-plant, but I think I have it all right this time. I expect to breed both

antilope and *cuama* from these eggs, as these forms are just beginning to appear."

As explained above, both pupæ emerged as *antilope*.*

D. *The Habits of the two Seasonal Phases of the South African Species of the Genus* Precis, *and the Stations which they respectively occupy.*

That these butterflies should exhibit a marked difference in habit and station corresponding to a difference in appearance at the wet, as compared with the dry season, is of such paramount importance in the consideration of the significance of these phenomena, that I quote at length all available observations of naturalists—some of them made before there was any suspicion that such forms as *sesamus* and *natalensis* were the two phases of a single species.

In "South African Butterflies," vol. i, London, 1887, p. 230, Mr. Roland Trimen, F.R.S., speaks of the habits of *Precis octavia* [*natalensis*, ⊕ wet phase], as he had seen it "widely spread over Natal in the summer of 1867. It frequents open, grassy hills, especially their summit ridges or highest points, and is very conspicuous, whether flying or settled."

Of the habits of *P. sesamus* ⊙ he writes (p. 233): "Though constantly to be seen flitting about with its congeners, *octavia*, *archesia*, and *pelasgis*, I have noticed that *sesamus* has a greater liking than any of them for shady places, preferring to settle under a bank or in some deep road-cutting. . . . The very dark bronzy-green under-side is well adapted for concealment in such spots."

Of *Precis archesia* (dry), he notes that it "delights to bask or repose on rocks or large stones. Colonel Bowker has noted that it sometimes congregates under rocks, and is often met with in small rocky caverns in deep forest kloofs." Mr. Trimen has noticed at Highlands, near Grahamstown, "a habit in the ♂ *pelasgis* [wet] which I have never witnessed in the case of *archesia* [dry], viz. that of perching himself on the projecting twig of some

* ["Although I am still of opinion that Dr. Butler is in error in regarding *antilope* and *cuama* as distinct species, yet it may be pointed out that the results of this experiment do not in any way disprove his contentions."—G. A. K. M.]

high bush at the edge of a wood, and thence giving chase to other passing butterflies" (p. 237).

In suggesting the seasonal relationships in the genus *Precis* which he afterwards proved to exist, Mr. Marshall speaks at the beginning of his first paper on the subject (Trans. Ent. Soc. Lond., 1896, p. 557) of the special interest which attaches to the alternations in this genus, "not only on account of the great differences in the colouring of their two forms, but also because of their marked change in habits."

He points out that the species of *Precis* in which there is but little seasonal change (*P. tugela*, *P. elgiva*, and *P. natalica*) are, when at rest, leaf-like in both phases, although they are more leaf-like in the dry season. He states that they are furthermore especially forest insects, being confined to "the warmer, low-lying, or heavily-timbered districts." The other species of *Precis* in which the seasonal forms are very different "occur more abundantly, or even exclusively, in the uplands and in open country." There are, however, differences of habit in the species of the former group. Thus Mr. J. M. Hutchinson is quoted by Mr. Marshall as stating that the summer form of *P. tugela* "is a bolder insect, sailing around and settling on trees at a fair height, almost after the manner of *Charaxes*, whereas the other is much more retiring, keeping among the thick bush and settling low down, or on the ground among dead leaves, etc." (*loc. cit.*, p. 558).

Turning to the second group of species in which the seasonal changes are pronounced, Mr. Marshall describes the habits of *P. simia* [*antilope*] (*loc. cit.*, p. 560): "The dry-season form only frequents the bush, settling on the ground among the dead leaves, or very rarely on small plants, the under-side colouring affording it excellent protection. As the season advances the habits of the insect change, and in October and November the later form (*c*) may be found in company with the early form of *simia* (*b*), frequenting open tops of kopjes, flying boldly about within a limited area, and settling with expanded wings on shrubs and bushes. This is the habit of all summer forms of *Precis*. . . ." With regard to *P. sesamus* ⊙, Mr. Marshall remarks that it "differs from the normal type of winter *Precis* in the absence of leaf-like colouring below, and in the very slight falcation of fore-wings. This

is accounted for by its different habits, for instead of frequenting dead leaves in the bush it prefers the dark rocks on stony and wooded kopjes." Evidence is brought forward to show that *P. artaxia* only exists in the cryptic dry phase in the warm timbered coast belt, although it develops a much less well-concealed wet-season phase (*nachtigalii*) in open country (pp. 561, 562).

In his second paper on the subject (Ann. and Mag. Nat. Hist., ser. 7, vol. ii, July 1898, p. 30) Mr. Marshall gives a further account of these interesting differences in habits: "Speaking broadly, the *natalensis* form frequents the highest points in any neighbourhood, especially if they be more or less open (for it is anything but a sylvan insect); whereas the *sesamus* form is more partial to shady spots, and is to be found in ravines and spruits or rocky wooded slopes, and shares with the Hesperid *Sarangesa dimidiata* a marked affection for disused mine-shafts and cuttings. This distinction must not be taken too strictly, for true *sesamus* is occasionally found in company with the summer form on open hill-tops, but principally at the change of seasons; but *natalensis*, so far as my experience goes, is never to be found in the more shady stations frequented by *sesamus*. The latter, moreover, is distinctly warier and more difficult of approach when not feeding, and if alarmed flies off with a rapid, and often zigzag, flight, settling abruptly among rocks or herbage, when its greenish-black under-side colouring is equally protective. *Sesamus* is more often observed in gardens, and not unfrequently enters human habitations in search of a shady resting-place." Mr. Marshall also quotes Mr. J. M. Hutchinson's experience on his farm in Natal, lying in an open plain between two ranges of hills: "He has found *sesamus* resident on the farm, occurring fairly commonly along the banks of the spruits during the winter, whereas *natalensis* is very much scarcer and non-resident, the examples seen having always been travelling from one range of hills to the other, on both of which it is common."

Since his return to England, in the present summer, Mr. Marshall has summarized his experience of the habits and stations of the seasonal phases of the species under discussion as follows:—

"There are three types of stations in South Africa which may be occupied by butterflies of this genus.

I. *Forest country*, with heavy timber affording deep

shade. Found on the coast belt and also in the interior, but, south of the Zambesi, only in patches.

II. *Woodland country*, without timber. Trees small, affording light shade.

III. *Open country*, without trees. Nothing higher than small scrub.

I. The following species are only found in the forest:—

1. *P. tugela*. It has been already explained that the wet-season form exposes itself more freely (p. 421). Both phases have leaf-like under-sides, but the dry has a more hooked tip to fore-wing and more prolonged anal angle to hind-wing.
2. *P. elgiva*. No difference in habits observed. The slight differences in appearance are due to a more hooked tip with a somewhat different direction, and a more leaf-like under-side in the dry phase as compared with the wet.
3. *P. natalica*. No difference in habits observed, both phases being low settlers. Ocelli and white spots on the under-side tend to disappear in the dry phase.

II. The following species are found in the woodland country:—

1, and 2, *P. antilope* and *P. actia*. In both these species the dry-season phase and the female of the wet are found in the more shady places, viz. the lower slopes of kopjes. The ♂ of the wet phase is usually found on the less-wooded higher slopes.

3. *P. artaxia*. The habits are like those of the two preceding species. Towards the forest belt in Umtali the dry phase encroaches on the wet, and in the low country between Umtali and the sea Selous never saw the wet form at all. The larger dry form has a *far* more leaf-like under-side, with a mid-rib, and hooked tip to the fore-wing, wanting in the wet. The dry phase is also more wary.

II. and III. The following species are found in open as well as woodland country:—

1, and 2, *P. sesamus* and *P. archesia* have very similar habits. The dry phase generally frequents the wooded and the wet phase the open country. In entirely open country the former would occur on the lower slopes in whatever shade is to be found. In entirely woodland country the dry phase would be found on

the lower, more shady slopes, the wet on the upper slopes where there is less shade.

III. The following species only occurs (in Mashonaland) in open country:—

1. *P. eryne*. Both forms are found in open swampy districts, without bush. Rare."

E. *Evidence of Adaptation in the conspicuous under-sides of the Wet-Season Phases almost equal to the proof of it in the cryptic Dry Phases.*

The evidence of adaptation in the cryptic under-sides of the dry phase in the species under discussion is so clear and so generally admitted that it is unnecessary to say much about it. I will only point to the manner in which the various distinctive elements of this phase are co-ordinated to a common end, that of concealment. Thus in the dead-leaf-like forms such as *archesia* and *antilope* we find the prolonged anal angle of the hind-wing, the produced and bent apex of the fore-wing, the angulated outline between these points, the stripe representing a mid-rib, the colours and patterns varying in different individuals but always resembling some type of dead leaf with discoloured blotches or eaten into holes (*archesia*). Most important of all there is the co-ordination of all these diverse elements with appropriate habits and the choice of an appropriate station. In *archesia*, which commonly frequents rocks, the intensely variable mottled appearance produces a strongly cryptic effect at a little distance, while a close inspection only brings out the details which produce a graphic representation of a dead leaf. In *sesamus* the outline and under-side differ from those of the dead-leaf-like dry phases of the other species, and differ in a direction which is specially cryptic, because of the peculiar habits of this phase of the species (see pp. 420, 422).

All this will be at once admitted by every naturalist who studies the specimens, as it is proclaimed by all who have had the advantage of observing the species in the wild state. What is not admitted, but is I think almost equally clear, is the fact *that adaptation in the opposite direction, viz. the direction of conspicuousness, is characteristic of the under-sides of the wet phase.* If the under-side merely reproduced the conspicuous pattern of the upper-

side of the wet phase the case would be strong and convincing for adaptation, and an interpretation based on the principles of warning colours or mimicry, Batesian or Müllerian. But the under-side does more than this; it differs from the upper-side, and so far as it differs, it becomes *more conspicuous*. The following details render the case for adaptation in the direction of conspicuousness, as it seems to me, overwhelming.

In comparing the upper- and under-side of the wet phase of the species to which the chief attention of naturalists has been directed, it is of special interest to turn to the accurate descriptions of Mr. Roland Trimen, F.R.S., written long before Mr. Marshall's discovery was thought of, a time when *natalensis* and *sesamus* were not only considered distinct but were even separated by *ecryne*. In "*Rhopalocera Africæ Australis*" (London, 1862–66) we read, on pages 130, 131, of *Junonia octavia* [*Precis sesamus*⊕]: "Under-side.—*Much paler, more creamy in tint, with a glistening pinkish tinge.*" Again, on the under-side of the fore-wing the author speaks of "the row of spots parallel to hind-margin commencing distinctly *from costa*, the first two spots increasing the number to seven; double row of bluish lunules more conspicuous than on *upper-side*, whiter." And the under-side of the hind-wing is thus described: "Basal black *containing four rather large, very conspicuous spots of the ground-colour*, and dusted with blue scales, which form a transverse streak between costal and subcostal nervures near extremity of black; whitish-bluish lunules, in hind marginal border, large and very conspicuous." The fact that the ground-colour of the under-side is much paler than the salmon-red of the upper and thus affords a far more effective contrast with the black markings is seen when Fig. 1 on Plate XIII is compared with Fig. 1*b* on Plate XII. Figs. 1 and 2 on Plate XII represent worn specimens, and the comparison with them is invalid. Fig 1*b*, Plate XII, possesses unusually heavy black markings, but the representation of the depth of the red ground-colour is normal for a fresh individual, as is that of the under-side in Fig. 1, Plate XIII. The more complete row of black spots and the greater conspicuousness of the border, owing to the larger white and blue markings in it, as described by Trimen, are also well seen when the figures are compared, but allowance must be

made for the fact that the border represented in Fig. 1*b*, Plate XII, is exceptionally broad, and is still more exceptional, indeed transitional towards *sesamus*, in the size of the blue markings in it. But the lighter character of the markings and the more conspicuous appearance of the under-side border is perfectly clear in Fig. 1, Plate XIII. And there is one other point not expressly mentioned although probably implied by Mr. Trimen, which is I think the most convincing evidence of all in favour of adaptation in the direction of conspicuousness;—the fact that the spots of ground-colour included in the basal black patch of the hind-wing, and absent from the upper-side, are distinctly lighter in tint than the rest of the ground-colour, and *thus afford a far more effective contrast with the black*. This difference in tint is well seen in Fig. 1, Plate XIII. The spot in the basal black of the fore-wing which represents a similarly-placed spot on the upper-side, is also often lighter than the rest of the under-side ground-colour, but the difference is far less marked than in the hind-wing and is sometimes absent.

Now the basal area of the under-side of butterflies' wings and especially of the exposed hind-wing is a part specially seized upon by natural selection for the display of conspicuous warning characters. It is seen in the red patches of many Pierine genera, especially the distasteful *Delias* (appearing also in its Chalcosid mimics) in the Old World, and several *Pierinæ* in the New, where Dr. F. A. Dixey has shown that the character has probably been adopted by *Heliconiinæ* in Müllerian association with them, the relationship—an important discovery first made in 1894 by Dixey—being one of "reciprocal assimilation" or "diaposematic resemblance" (Trans. Ent. Soc. Lond., 1894, pp. 296–298; 1896, pp. 72–74; 1897, pp. 326, 327, 331; Proc. Ent. Soc., 1897, p. xxix). A stripe of bright yellow or red bordering the basal part of the costal margin of the under-side of the hind-wing of a large number of distasteful tropical American butterflies of different sub-families is another very characteristic synaposeme, rendering the same part of the wing especially conspicuous. And in Africa itself we have the most remarkable case of all, in the triangular golden-brown, black-marked synaposeme which is discussed at some length on pages 488 to 490 of the present memoir. Furthermore, there is the group

of large black spots on a light ground which renders this part of the wing prominent in such large numbers of Ethiopian butterflies.

In the wet phase of *Precis sesamus* this area is also remarkably conspicuous, but by a method which is as positive to negative in relation to other distasteful butterflies inhabiting the same part of the world, viz. by the appearance of light spots on a black ground, instead of black spots on a light ground.

Thus it is improbable that this particular element in the conspicuous appearance of the under-side of the wet phase of *P. sesamus* can be mimetic, and its existence, side by side with a general resemblance in colour and pattern to a large *Acræa*, is evidence that such resemblance is Müllerian or synaposematic rather than Batesian or pseudaposematic. This argument is much strengthened by the discussion of the wet phase of the allied *P. archesia* (see pp. 428–430).

Much that has been said of *P. sesamus* applies with greater force to the closely-allied *P. antilope*. On comparing the under-side of the wet phase, shown in Fig. 4, Plate XIII, with the upper-side of the same specimen, shown in Fig. 3, Plate XII, it is at once seen that the difference in tint of the ground-colour and in conspicuousness of the marginal band on the two wing surfaces is far more pronounced than in the species which has been just described. In fact, with an upper-side which is much less conspicuous than *sesamus* ⊕ (compare Figs. 3 and 1*b*, Plate XII: it must be remembered that the ground-colour of 3 is merely tawny, while that of 1*b* is salmon-red), the wet phase of *antilope* combines an under-side which is distinctly more conspicuous than that of the corresponding form of the allied larger species (compare Figs. 4 and 1, Plate XIII). The increased conspicuousness is especially clear in the relative size of the spots in the basal black patch and the inclusion in it of a very large piece of the ground-colour of the fore-wing. Here too the increased lightness of the spots of ground-colour in the black area is often distinct, as it is in Fig. 4, Plate XIII, but in a large proportion of the individuals I have had the opportunity of examining it is only feebly marked.

In *P. antilope* ⊕ there is probably some considerable synaposematic approach towards the *Acræa* type, but to a less extent than in *P. sesamus;* while the conspicuous basal

character which is non-acræiform and purely aposematic is far more emphasized than in the latter species. It is probable that *sesamus* represents a later development, and that in it the synaposematic elements have been gradually strengthened and the peculiar aposematic character correspondingly reduced.

We now pass to the consideration of a species in which the conspicuous characters of the under-side of the wet phase are probably entirely peculiar and aposematic.

Mr. Marshall's suggestion in 1896 that *Precis pelasgis* is the wet phase of *P. archesia* has never been confirmed by breeding the one form from the other. It is, however, certain that his conclusion was sound. The two forms have often been captured *in coitu*. The female *pelasgis* represented in Plate XII, fig. 4, was captured by Mr. Marshall *in coitu* with the male *archesia* shown in Fig. 5 of the same plate. Intermediate forms are much commoner than in the case of *sesamus* and *antilope;* and above all the relationship of wet phase to dry is far closer in *archesia*, so that it is possible to see how the one was derived from the other more fully than in any of the species with markedly-different seasonal forms. The under-side of one of the commonest forms of the dry phase is represented in Fig. 6, Plate XIII, and opposite to it that of the typical wet phase in Fig. 5. At first sight they appear totally different, and certainly the latter is as conspicuous as the former is well concealed. An uncoloured illustration cannot do justice to the varied shades of brown and grey on the under-side of *archesia* (Fig. 6), and a long series of specimens would be required to show the immense range of individual variation by which all kinds of common appearances presented by dead leaves are reproduced. Among such variations is one in which the dark-brown ground-colour is almost uniform and unmottled inside the mid-rib-like stripe (Fig. 7). From this we pass to forms in which the stripe widens into a light band (Fig. 8), clearly showing its homology with the still more conspicuous band of *pelasgis* (compare Figs. 5 and 8). Such a variety as that shown in Fig. 8 is still a long way on the *archesia* side of a form intermediate between the wet and dry phase, and would certainly be cryptic rather than conspicuous in nature, although not so well concealed as the form shown in Fig. 7, and still less so than that shown in Fig. 6. Truly intermediate varieties between the wet and dry phases are not uncommon, in which

the broad band becomes sharply defined on its outer border, but lacks the light tint of the full wet phase.

These considerations and the careful comparison of Figs. 5 to 8 on Plate XIII will show the essential nature of the changes by which the cryptic under-side of the dry phase is converted into the startlingly conspicuous under-side of the wet phase, or *vice versâ*. The mid-rib-like stripe widens, lightens in tint, becomes sharply defined along its outer border, and is now the "warning band" of *pelasgis*. The row of ocellated spots, many of which, with semi-transparent white centres and specially-coloured borders, suggest holes in the apparent leaf of *archesia*, become entirely or almost entirely black upon the hind-wing, and gain intensely black borders upon the fore-wing of *pelasgis*, and, placed upon the light ground of the "warning band," render this feature still more conspicuous. The mottling disappears, and the ground-colour, both within and without the borders of the "warning band," becomes an almost uniform very dark brown, forming a most effective contrast with the band. Finally, the dead-leaf-like margin of the wing of *archesia* is rendered conspicuous in *pelasgis* by a black-and-white fringe and two parallel series of light markings just within and parallel to the much less deeply indented outline.

Furthermore, the comparison of Figs. 6 to 8 on Plate XIII with Fig. 5 on Plate XII shows clearly enough that the under-side of the dry phase of *archesia* differs from its upper-side in being cryptic, while the comparison of Fig. 5 on Plate XIII with Fig. 4 on Plate XII shows that the under-side differs from the upper-side of the wet phase (*pelasgis*) in being more conspicuous, thus in both respects acting like the two phases of *sesamus* and *antilope*. The under-side of *pelasgis* is more conspicuous than its upper-side because of the increased lightness and greater sharpness of the borders of the band and the greater contrast afforded by a darker ground-colour, also because of the more pronounced light marginal markings.

I have described the relationship between the phases of *archesia* at some length, because it was the consideration of this species which first convinced me of the validity of the interpretation here set forth, that we have convincing evidence of natural selection acting in two opposite directions in the two phases—in the one to produce the maximum of concealment, in the other a very efficient form of

conspicuousness. When I realized that it was the mid-rib-like stripe—the character which more than any other gives meaning to the cryptic resemblance to a dead leaf; that it was this very character which, transformed into the "warning band," became the conspicuous feature of the wet phase—the operation of natural selection seemed as clear in the one case as the other.

When we examine the species of the whole genus *Precis* and those of the genera allied to it, the conclusion is forced upon us that the dry cryptic phases are ancestral as compared with the conspicuous wet phases. I do not mean to imply that the cryptic forms have not altered, but that the original form of the species possessed a cryptic under-side, which has been handed down with more or less change as the cryptic under-side of the existing dry phase, while the conspicuous under-side of the existing wet phase is a new and comparatively recent development. This question of the relative age of the two forms is most important and interesting, and from the very first occupied Mr. Marshall's attention. Thus the following passage is extracted from a letter written a few weeks after his discovery:—

"*Salisbury, June* 5, 1898.—I should be most interested to learn your ideas as to the reasons for the singular seasonal change in this species, for I must admit that I cannot arrive at any really satisfactory conclusion on the subject as yet. The blue scales of *sesamus* are my chief stumbling-block, for I certainly cannot perceive what utility they can possess, and considering its protective under-side colouring there seems no reason why it should not have retained its wet-season colours above, as in the case of *P. artaxia* or *P. ecrync.* I suppose you will agree that *sesamus* is a later development?"

For the reasons I have indicated above it is difficult to doubt that the cryptic character of the under-side of *sesamus* is ancestral and the conspicuous under-side of *natalensis* relatively recent, but with regard to the upper-sides this conclusion is by no means so evident. Indeed on comparing the species with *antilope* and other allies, it seems probable that the upper-side of *natalensis* is more ancestral than that of *sesamus*, having been chiefly modified in tint, thus falling into Müllerian association with the larger Acræas. The upper-side of *sesamus* probably shows cryptic changes in the acquisition of the far darker

colours which render the phase less conspicuous in the stations it frequents.

There does not seem to be any escape however from the conclusion that the conspicuous under-sides of the wet phases are relatively recent, and if this conclusion be considered in relation to the comparison between the under-sides of *archesia* and *pelasgis*, it leads inevitably to the conclusion that the *conspicuous* appearance of the one *has* been modified out of the older cryptic appearance of the other, and not *vice versâ*.

On what hypothesis can we believe that such a change has taken place? In the existing state of our knowledge there are only two possible interpretations: (1) that the modification is mimetic of some other conspicuous distasteful form; (2) that it is a warning of some special protection possessed by the *Precis* itself. The former interpretation cannot apply to the case of *pelasgis*, because its pattern is so unlike that of the well-known distasteful Ethiopian Rhopalocera, although some advantage may be gained by Müllerian association with black and white aposematic genera such as *Amauris, Neptis, Planema*, etc. Furthermore, it has been shown that there are important elements in the conspicuous under-sides of the wet phases of *sesamus* and *antilope* which are not synaposematic, although the appearance as a whole is probably to be explained in this way. I therefore firmly believe that the conspicuous appearance of *pelasgis* has been produced by selection from the cryptic *archesia* as a warning character indicative of some special protection, an aposeme proclaiming that it is less palatable or in some way less suitable as the food of insect-eating animals than an immense number of other species which abound during the wet season in the same stations.

I proved in 1887 (Proc. Zool. Soc., p. 191) that the likes and dislikes of insect-eating animals are purely relative, and that a conspicuous distasteful form will be freely eaten under the stress of hunger, that the existence of these forms depended entirely upon the co-existence in their neighbourhood of an abundance of palatable species, that under any other circumstances the warning colours if freely exposed would be a danger and would lead to the extermination of the species. As soon as I had studied the case of *archesia* and *pelasgis* I felt convinced that the

extraordinary seasonal phases of *Precis* were to be interpreted along the lines suggested in 1887—that we have to do with a set of somewhat distasteful species which can only exist in the keen struggle of the dry African winter when food palatable to insect-eaters is relatively scarce, by a very high standard of protective disguise associated with the appropriate instincts, but gain the recognized advantages of aposematic colouring by producing markedly conspicuous generations during the moist summer, when insect-eating animals have a much greater variety and abundance of suitable food.

F. *The severity of the Struggle for Existence among Insects in the African Dry Season as compared with the Wet. The relation of the Seasonal Changes in* Precis *to those of other Butterflies.*

As soon as the idea expressed in the concluding paragraph of the last section of this memoir occurred to me, I wrote to Mr. Marshall asking for his experience on the subject, and also inquiring whether any of the admittedly unpalatable African butterflies exhibited seasonal changes, such that the winter generations became comparatively inconspicuous.

His deeply-interesting reply is printed *in extenso* below.

"*Salisbury, Jan.* 8, 1899.—As to your query about the keenness of the struggle for existence at the two seasons, in my own mind I had never felt any doubt that the dry season is certainly the more critical period for insects, and this I referred to incidentally in my paper on *Precis* (Ann. and Mag. Nat. Hist., ser. 7, vol. ii, July 1898, p. 36). It is true that insectivorous birds are far more numerous during the summer, but this I think would be more than outbalanced by the increase of such insects as Coleoptera, Hymenoptera, Diptera, etc., apart from the fact that the summer broods of the perennial butterflies are undoubtedly larger and much more numerous (some *Pierinæ* have a fresh brood every four or five weeks), and that a number of additional species make their appearance at that season only. On the other hand, during the dry season, although a number of migratory birds depart northwards, yet we have a considerable number of resident insectivorous birds, including rollers, drongos, shrikes, flycatchers, bush-king-

fishers, etc., and owing to the warmth of the midday sun, even in mid-winter, the lizards are always more or less active, and the insectivorous mammals are probably in no way reduced. With the insects it is very different; owing to the parching up of the vegetation the hosts of phytophagous insects disappear almost entirely, and the diminution in insect-life is enormous, being most noticeable among the Coleoptera and least so among butterflies, of which latter almost two-thirds have winter broods; and moreover their lives would be rendered even more precarious by the generally adverse conditions of their environment from climatic causes. It therefore seems clear that the struggle for existence would fall pretty severely on butterflies during the winter, owing to their general conspicuousness, and that such is actually the case is shown by the numerous instances of the development of a highly-protective under-side coloration during the dry season among *Satyrinæ*, *Nymphalinæ*, *Lycænidæ*, and *Pierinæ*. That the struggle is sufficiently keen, however, to compel unpalatable species to adopt protective coloration I should not like to say. The following is, I take it, a complete list of the South African genera possessing more or less undoubted distasteful qualities: *Limnas*, *Amauris*, *Acræa*, *Planema*, *Pardopsis*, *Neptis*, *Pentila*, *Alæna*, *Mylothris*, and *Pontia hellica*, and with the exception of *Acræa* none of these exhibit any change of colour during the winter which can possibly be construed as protective. Dealing therefore with *Acræa*, I find that even in this genus a considerable number of species such as *horta*, *neobule*, *anemosa*, *acara*, *encedon*, *cabira*, etc., exhibit only a comparatively insignificant seasonal dimorphism or even none at all. There remains therefore a group composing such insects as *violarum-asema*, *nohara-halali*, *petræa*, *doubledayi-axina*, *atolmis*, *buxtoni*, etc., in which the dimorphism is fairly strongly marked in one sex or the other, and an interesting feature about this group is that they are all, with the exception of *petræa*, frequenters of open country, having a low flight and frequently sitting on the ground. It is also noticeable that this group, unlike the other, presents a very marked difference in the sexes, and wherever this is not the case, both sexes have a distinctly obscure coloration as compared with their congeners, *e. g. axina* and *asema*; further, that where the summer males exhibit any exceptional brilliancy, as *petræa*, *atolmis*, or

nohara, it is always compensated for by an exceptional dulness on the part of their respective females. I fear I do not feel sufficiently competent to attempt an explanation of the above facts, but I think you will agree that as a whole they hardly bear out the suggestion that distasteful species are compelled to adopt protective colouring in winter through the keener struggle for existence; and for the present I am tempted to incline to the view that the less marked cases of dimorphism may be attributable to purely climatic causes. The colouring of the other open veldt *Acrææ*, viz. *halali*, *axina*, and *asema*, is somewhat puzzling; for in the two latter it is far from being very brilliant or conspicuous; in *halali*, the male in summer is very brilliant, but the blackish or brownish grey of the female is certainly protective, and the insect when alarmed is very hard to follow with the eye in its low dodging flight over the herbage. In the winter the colouring of both sexes of all three species is certainly not very conspicuous among the withered grass. Either their unpalatability must be of a low order, or else they must be more subject to attack by some particular enemies than the woodland species. I should not be surprised if the rollers, of which we have five species, or cuckoos (also five) were to eat Acræas, as they are all far from particular as to their diet."

This hypothesis concerning certain of the smaller Acræas had been in Mr. Marshall's mind for a long time. Thus he wrote in 1896 from Natal:—

"*Estcourt, Oct.* 15, 1896.—I have an idea that all the species of the genus *Acræa* are not protected equally by nauseous taste, etc., and some of them perhaps not at all; for in many of the smaller species there is a marked seasonal dimorphism which has clearly a protective value. Now such a change seems hardly in keeping with warning coloration, which must be constant to impress itself on the minds of enemies, and moreover a species which requires protection by seasonal dimorphism cannot be very much protected in other ways, not to mention the fact that its colouring cannot be both warning and protective at the same time. There is, of course, nothing to show how much of the seasonal change we can attribute to climate alone. For instance, in comparing the slight alteration in an *A. acara* with the marked change in female *A. petræa*, are we to suppose that the dark-grey female of the latter

is due solely to climatic influence, and that such a change in the former is checked by the necessity for keeping the warning coloration uniform, or are we to consider that the slight change in the former is all that climate can effect, and that in the case of *petrea* this slight climatic effect has been enhanced by some other cause—presumably protection? Personally I incline to the latter view, but in either case it is clear that there are varying grades of protection by distastefulness in the genus."

An extract from another letter states the same important conclusions as to the severity of the struggle during the dry season.

"*Salisbury, March*, 10, 1898.—There are very few butterflies (South African, at least), exclusive of the admittedly protected species and their mimics, of which the bright colour cannot be explained on the *Teracolus-Kallima* basis. The most evident exceptions are *Byblia*, certain species of *Precis*, as *sesamus* (form *natalensis*), *ceryne*, etc., which are practically coloured the same below as above, and *Belenois severina* and *mesentina*. The first I will admit has been so far a stumbling-block to me, though I am not yet prepared to accept it as a protected species. Provided that my ideas on seasonal variation in *Precis* be correct, these would also fall under the same heading as *Teracolus*, for like them they only assume the protective under-side colouring during winter, when attacks from birds are no doubt a great deal more to be feared, owing to the almost complete absence of *easily-caught* prey, such as beetles and other small insects; the summer forms probably are very little molested by birds, owing to their great agility and alertness, and the profusion of other insects at that period; they do, however, not unfrequently fall a prey to the rock-lizards, which stalk them with much astuteness, as I have observed on several occasions.

"With regard to *Belenois* my mind is still open, for it is a very curious genus, containing as it does the above two species which might perhaps from certain considerations be considered protected, and at the same time a species like *B. gidica* which evidently comes under the *Teracolus* heading, and lastly *B. thysa* which, to my mind at least, is clearly a Batesian mimic."

After a consideration of the evidence brought forward above, it will be generally admitted that the struggle for

existence is far keener in the dry winter season, and that butterflies are especially subject to it.

The most distasteful forms, many of which are the models for mimicry, are sufficiently protected to retain their conspicuous aposematic appearance throughout the year, and either exhibit no change in the winter season or a change which is not in any way cryptic.

While this is true of all the larger and most conspicuous Acræas, some of the smaller Acræas do exhibit changes in a cryptic direction in their winter generations. These are Acræas which, from their colouring and habits, may be inferred to possess only a moderate degree of unpalatability as compared with the other species of the genus.

Cases in which colouring is "warning and protective [procryptic] at the same time" are quite common, *e. g.* the protected larvæ of many *Tenthredinidæ* which harmonize sufficiently well with their food-plant to be concealed at a little distance, but assume the most conspicuous aposematic attitudes and movements as soon as they are discovered and disturbed. But in the case of the smaller Acræas suggested by Mr. Marshall, the colouring which is most procryptic does not occur at the same time as that which is less procryptic or probably aposematic. Mr. Marshall's numerous experiments upon the edibility of the smaller Acræas (see Sections 9, 18, 19) do not support the view that any of them are palatable to the insect-eating animals made use of. It has already been pointed out that the refusal or evident dislike of insect food by captive animals is trustworthy evidence of unpalatability, while acceptance is not proof of palatability (see p. 317). The smaller Acræas furthermore fall into beautiful syn-aposematic groups (see pp. 492, 493); indeed a strong Müllerian association can be recognized throughout almost the whole of the Ethiopian representatives of the genus, as was first suggested by Professor Meldola (Ann. and Mag. Nat. Hist., ser. 5, vol. x, 1882, p. 425).

It is therefore probable that these smaller Acræas are still specially protected, although to a less extent than other species of the genus, but that the keener struggle of the dry season has compelled them to produce generations which are inconspicuous as compared with those of the wet season.

If these interpretations here suggested be correct, the parallelism with *Precis sesamus*, etc., is very remarkable.

In the *Acræinæ* we find that the least unpalatable species of an unpalatable and conspicuous family have been compelled to produce relatively inconspicuous generations in the severe struggle of the dry season: in the *Nymphalinæ* we find that some of the less palatable species of a comparatively palatable and inconspicuous family have been compelled to produce strongly conspicuous generations in the wet season when more edible insect food is abundant.

The interpretation I have here suggested was put forward very cautiously in a note, dated Nov. 1898, to a short paper on Mr. Marshall's results with *P. sesamus* in the Proc. Ent. Soc. Lond., Oct. 5, 1898, pp. xxv, xxvi. The note points out that insects with warning colours are not to be seen in an English winter. "Those such as *Coccinellidæ*, which exist in the perfect form, hide themselves. The reason probably is that the amount of palatable food available is not sufficient to make it safe to rely on unpalatability, accompanied by warning colouring [see also 'Colours of Animals,' London, 1890, pp. 179, 180]. Experiments with hungry animals support this view. It is possible that the conditions are similar in South Africa [it is perhaps unnecessary to state that *organic* conditions were alone referred to], and that warning colours are more characteristic of the wet than of the dry season, thus affording greater opportunities for mimetic resemblance. If it should hereafter be shown that *Precis* is to some extent unpalatable, and that its resemblance to an Acræan type is synaposematic rather than pseudaposematic, the parallelism with our own fauna would be even closer, the conspicuous species which hide and thus adopt procryptic habits being represented by one which gives rise to another brood with markedly procryptic colouring and habits."

Mr. Marshall in commenting on this note records the following interesting observations on the habits of South African Coleoptera as determined by damp and dryness.

"*Salisbury, Feb.* 12, 1899.—Do you think that the English *Coccinellidæ* really hide in winter owing to their increased danger from enemies, and not from climatic causes? I ask the question because in this country Coleoptera are highly susceptible to weather. They appear to be for the most part absolutely dependent on moisture, this being especially noticeable among the terrestrial forms such as *Cicindelidæ, Carabidæ, Psammodes,*

Anomalipus, etc. These insects appear with a rush as soon as the early rains have saturated the ground, but should a dry spell supervene, they disappear as rapidly as they came, only to emerge again on the recurrence of a good rain. The case of the dung-beetles has always puzzled me, for here we have a large family of powerful and apparently hardy beetles, which have a constant supply of food all the year round, and yet they are unable to stand out the winter in the imago state, although a delicate butterfly can do so. In fact, the *Copridæ* are quite as dependent on moisture as the large *Carabidæ*, and are only to be seen at work from November to March, retiring even then during the dry spells."

The interesting effects of dryness described above certainly cannot be produced in our damp winters, and it is difficult to believe that our cold can be the cause of the retirement of *Coccinellidæ*, etc., when species of insects closely allied to those of England can endure to be frozen stiff and brittle in a temperature of 50 degrees below zero (F.) in a Manitoban winter.

Another letter from Mr. Marshall, received about the same time, contains a different comment upon the interpretation suggested by the present writer in 1898 and here amplified.

"*Salisbury, Jan.* 8, 1899.—I can fully perceive that any arguments that may be brought forward in support of the contention that *Precis sesamus* (*natalensis* form) is an example of incipient mimicry are equally applicable to the suggestion of incipient warning coloration, and for the present it must remain a matter of opinion as to which is the correct explanation, though the alertness of the insect and its undoubted palatability, so far as lizards are concerned, seems to lend more support to the former view to my mind." [See also Ann. and Mag. Nat. Hist., ser. 7, vol. ii, July 1898, p. 35.]

It has been here shown that there are important elements in the under-side coloration of the wet phases of *Precis sesamus* and *P. antilope* which cannot be explained as mimicry, Batesian or Müllerian (see pp. 425–8), while the entire appearance of the under surface of *P. archesia* form *pelasgis* can only be interpreted as a warning character (pp. 428–431).

The conspicuous appearance of the under-sides of these forms is doubtless chiefly adapted to render them con-

spicuous during the attitude of rest. There is probably a certain parallelism with cryptic under-sides, such as those of our *Vanessidæ*, which have no particular meaning in flight and when the insect alights, but still remains fully on the alert. The *resting attitude* is specialized in relation to the development of cryptic colours and patterns on the under-side, and in this attitude cryptic insects are always inconspicuous. Apart from the evidence of adaptation in the direction of conspicuousness on the under-side of the wet phases of *Precis*—the strongest argument for the presence of some distasteful quality—the mere existence of such an appearance in a palatable species is inconsistent with the explanation of cryptic under-sides as the product of adaptation in the direction of concealment from enemies.

The successful attacks of a species of lizard may be analogous to other well-known instances in which special enemies, such as the cuckoo, are known to devour conspicuous unpalatable insects.

Two other arguments in Mr. Marshall's paper (Ann. and Mag. Nat. Hist., ser. 7, vol. ii, July 1898, p. 30) must be met here. First, the suggestion that the brilliant colours of *natalensis* are due to the impunity with which such a development can arise in the limited struggle for existence in the stations occupied by the species, and the abundance in the wet season of other insect food (*loc. cit.*, pp. 35, 36). Such a suggestion does not explain the under-side coloration, and especially the evidences of adaptation in it. Secondly, Mr. Marshall meets de Nicéville's and Weismann's contention, that both seasonal forms "must be adaptive, otherwise the non-adaptive form would be gradually supplanted by its more favoured relative," by the suggestion that the dry-season phase may be a recent development which is even now actually supplanting the wet phase (*loc. cit.*, pp. 36, 37). It is, however, difficult to believe, looking at the *Nymphalinæ* as a whole, and especially the nearest allies of the species under discussion, that the conspicuous under-side of the wet phase is ancestral, and the cryptic under-side of the dry phase recent (see p. 430), so that the argument set forth above seems to me untouched. Mr. Marshall has indeed shown that the dry phase of *P. artaxia has* actually supplanted the wet phase (*nachtigalii*) in forest regions, where the struggle for existence is far more uniform at all seasons of the year than it is in the more open woodland country

in which the dry and wet phases alternate. The displacement of one form of *artaxia* by another is however no evidence of relative age, but only of relatively better adaptation to the conditions which obtain in the area where the displacement has occurred. Hence the observation recorded by Mr. Marshall seems to me strongly to confirm de Nicéville's and Weismann's conclusion that when both seasonal phases exist, both are adaptive.

Mr. Marshall also shows on pp. 421 to 423 that the species of *Precis* entirely restricted to forest regions possess cryptic under-sides and habits all the year round, although the dry-season generations are more completely cryptic.

It is not difficult to understand the observations referred to above,—viz. that the appearance and habits while cryptic all the year round should be more cryptic in the generations of greatest stress. Thus Mr. Marshall describes the wet-season phase of the purple-tipped South African *Teracoli* as having under-sides not specially well adapted for concealment on the ground during the resting attitude, and without the habit of suddenly settling when pursued, modes of concealment adopted by the dry-season generations. In such examples the success of the adaptations may be equal in the two seasons because of the difference in the intensity of the struggle. But the extreme seasonal phases of *Precis* can never be thus understood, because the wet forms are not merely less cryptic than the dry, they have gone over into the opposite camp, and have developed a very extreme, and, except in the examples of mimicry and warning colours, an unknown degree of conspicuousness.

Another and very interesting form of seasonal dimorphism is that which has been well known for a long time in the *Satyrinæ*, and consists chiefly in the development of conspicuous ocelli, especially upon the under-side of the wet phases and their greater or less suppression in the dry. No interpretation of the change has, so far as I am aware, been attempted, except that of Portschinski, which has been further alluded to and criticized on p. 398. I think it is probable that a valid interpretation is suggested by the result of an experiment made in 1887, and witnessed by Professor Meldola as well as by me. A specimen of *Canonympha pamphilus* was introduced into a lizard's cage. "It was at once obvious that the lizard was greatly interested in the large eye-like mark on the under-side of the fore-wing: it examined the mark intently, and

several times attempted to seize the butterfly at this spot. The observation seems to point to, at any rate, one use of the eye-like markings which are common on the under-sides of the wings of butterflies," viz. in order to attract the attention of an enemy, and thus divert it from more vital parts ("Colours of Animals," London, 1890, pp. 206, 207). The same interpretation is suggested by the habits of many species which expose an eye-spot as soon as they settle, when they are likely to be seized by an enemy which has marked them down to their resting-place, but quickly lower the wings and conceal the spot, so that they are far more likely to be concealed from an enemy which has not been specially directed to the exact place by seeing them alight. (Much confirmation will be found on pp. 371–5, where Mr. Marshall's injured specimens are described.)

Such directive marks may well be an advantage in the wet season, when enemies with an abundance of other insect food are less keen in their pursuit of butterflies, but in the far greater stress of the dry season we can understand how they would become a danger, and how the only chance of the survival of the species lies in the adoption of a cryptic appearance, and cryptic instincts in their most extreme and unqualified form.

This explanation has much in common with that suggested for the seasonal phases of *Precis*. Indeed, it is of much interest to observe that *nachtigalii*, the wet form of *P. artaxia*, has precisely the same relationship to the dry form as that described above in *Satyrinæ*. It is far less cryptic than the leaf-like dry phase, but it is not conspicuous. The ocelli on the under-sides of both wings and the strongly-marked hind margins, together with the specially prominent apex of the fore-wing, are probably directive characters which divert the attention of an enemy from the vital structures, when the insect is at rest with its wings closed.

The relationship of the interpretation in *Precis* to that just suggested in *Satyrinæ*, and to that offered in certain smaller Acræas (see pp. 433–7), renders it on the whole improbable that there is any alternation in degrees of unpalatability corresponding to the alternation in the seasons. There is, however, no *à priori* difficulty in the hypothesis that a higher degree of unpalatability may be correlated with the conspicuous colouring of the wet phase of *Precis;*

and experiments specially undertaken in order to test the suggestion would be of much interest. That the hypothesis is improbable is further shown by a long series of experiments (hitherto only published in abstract in the Report of the British Association, Manchester, 1887, p. 763) which I conducted in 1887 with lizards and the highly insectivorous marmoset. Large numbers of the imagines of *Vanessa io* and *V. urticæ* were made use of, and I came to the decided conclusion that both were somewhat unpalatable. They were certainly only eaten when the insect enemies under observation were hungry. Now the strongly cryptic under-side of both species associated with a fairly-conspicuous upper-side renders them in every way comparable to the dry phases of *Precis*. The results of my experiments suggest that if *Vanessa urticæ* appeared on the wing in the teeming organic environment of Africa in the wet season—with far more enemies but an even greater preponderance of palatable insects—it would be to its advantage with its present degree of unpalatability to acquire a conspicuous under-side coloration, and thus to ensure easy recognition and rejection with comparatively little loss of life by experimental trials.

The considerations set forth above suggest what will probably hereafter be proved to be true, that a degree of unpalatability associated with a conspicuous appearance in the tropics will often appear associated with a cryptic appearance in the Holarctic Belt as well as in those areas of the tropics in which for special reasons the amount and variety of insect life is greatly restricted.

It is suggested on pages 475 to 477, that this is the interpretation of the loss of much of the aposematic appearance of *Limnas chrysippus*, var. *klugii*, on desert areas in the tropics.

To return to the seasonally dimorphic Ethiopian species of the genus *Precis*, if the two phases have been produced, as is here contended, by natural selection working in opposite directions because opposite kinds of adaptation are advantageous in the very different organic environments of the wet and dry seasons, the questions as to the way in which the change is actually determined, and as to the existence of any kind of susceptibility to external influences connected with the seasons, are still unanswered. The considerable amount of labour devoted by Mr. Marshall to the solution of this problem has up to the present

yielded negative results. Before describing his experiments and discussing the results, it is desirable to show the mode of succession of the phases in the wild state. By far the most complete evidence I have been able to obtain relates to a single species, *P. sesamus*.

G. *The succession of the two Seasonal Phases of* Precis sesamus *in Nature.*

The following extracts from Mr. Marshall's letters from 1897–1900 give an account of his experience of the succession of wet and dry forms of this species in the wild state, and also show how the conviction was gradually forced upon him that the early appearance of occasional specimens of the dry phase in the heart of the wet season is not due, as he thought at first, to exceptional climatic conditions (see also his paper in Ann. and Mag. Nat. Hist., ser. 7, vol. viii, Nov. 1901, p. 402).

"*Malvern, Natal; March* 12, 1897.—You will notice that the dry forms of several species made their appearance at the Karkloof in the middle of February: this is most unusually early. I do not know whether it is a feature and characteristic of that locality or whether it is due to the abnormally dry weather during that month, which is usually one of the wettest in the year. The average rainfall for this February was considerably lower than it has been for twenty years. It is true that *here* the insects are still all of the true summer form, but the proximity of the sea may account for that."

"*Salisbury, March* 6, 1898.—*Sesamus* was unusually early here this year, appearing at the beginning of February, full six weeks before its usual time. This I am inclined to attribute to the exceptionally dry January and February we have had—normally our wettest months—though I am aware that Weismann considers that exceptional seasons have little or no effect on seasonal forms, which certainly does not accord with my experience in S. Africa."

"*Salisbury, Feb.* 12, 1899.—I send a specimen of *P. sesamus* ⊙ captured on Jan. 27, 1899, on which day I also saw another. These two examples are of considerable interest as bearing on the problem concerning the stimulus which actually induces seasonal change in this species.

In a normal wet season (in which there are more or less continuous heavy rains from the middle of December to the end of February) *P. sesamus* ⊙ appears at the end of March. Last season we had heavy rains up to the end of December 1897, but January was unusually dry and *sesamus* ⊙ appeared on Feb. 6, being the earliest record I had for it. This season the drought was still more severe in January and commenced earlier, viz. about Dec. 12. This has been accompanied by a still earlier appearance of *sesamus* ⊙. The evidence so far as it goes tends to show that climatic conditions, in some cases at least, are directly capable of inducing the change and upsetting the normal alternation of the forms. Here, owing to highly abnormal conditions, we have the dry form occurring at what is normally the very height of the wet season. Moreover, ever since I have observed seasonal dimorphism in butterflies I have noticed the effect of abnormal weather in retarding or accelerating the appearance of either form, and Barker has made similar observations at Malvern, near Durban, Natal."

"*Salisbury, April* 25, 1899.—The *sesamus* form is evidently more dominant than the *natalensis*, for despite the heavy rains in February 1899 the latter made very little headway after the appearance of the dry-season form; whereas among such insects as the *Pierinæ* the result of the alternating extremes was much more evident."

"*Salisbury, Feb.* 7, 1900.—In spite of our heavy rains during January (16·75 inches for the month) the winter forms of *Precis* are appearing just as early as last year, which has puzzled me considerably. I shall send you the first examples of each form captured."

"*Salisbury, June* 26, 1900.—I am afraid I am not yet convinced as to the automatic alternations [viz. due to the organism itself and not to external stimuli] of the seasonal forms in *P. sesamus;* there seems to be at present an equal amount of evidence on either side, and until the matter can be settled by an exhaustive series of experiments I must retain an open mind on the question."

I have given below a list of all the specimens of the two phases of *Precis sesamus* sent to me from Mashonaland by Mr. Marshall.

LOCALITY.	OBSERVER.	DATE.	FORM OF *Precis sesamus* IN HOPE COLLECTION.
Mazoe, 4000 ft.	G. A. K. Marshall.	Dec. 28, 1894.	1 *natalensis*, fresh.
Gadzima, 4200 ft., Umfuli River.	G. A. K. Marshall.	Dec. 20, 1895.	1 *natalensis*, fresh.
		Dec. 23, 1895.	3 *natalensis*, fresh.
Salisbury, 5000 ft.	G. A. K. Marshall.	March 20, 1895.	1 *sesamus*, fresh.
		Feb. 13, 1898.	2 *natalensis* (in coitu). ♂ worn, ♀ fresh.
		Feb. 20, 1898.	1 *natalensis*, fresh.
		Feb. 27, 1898.	1 *natalensis*, worn (parent of 1 *sesamus*, and 1 *natalensis*).
		March 2, 1898.	1 *sesamus*, fresh.
		March 6, 1898.	1 *natalensis*, worn (parent of 1 *sesamus*).
		March 12, 1898.	1 *sesamus*, fresh.
		March 16, 1898.	1 *sesamus*, fresh.
		April 2, 1898.	1 *sesamus*, fresh.
		Jan. 27, 1899.	1 *sesamus*, fresh (the first seen in 1899).
		March 11, 1899.	1 *natalensis*, worn.
		Feb. 3, 1900.	1 *sesamus*, fresh (the second seen in 1900).
		Jan. 23, 1901.	1 *natalensis*, fresh.
		Jan. 26, 1901.	1 *sesamus*, fresh (the first seen in 1901).
		March 2, 1901.	1 *sesamus*, fresh, transitional towards *natalensis*.
		April 8, 1901.	2 *sesamus*, fresh.

A study of the above list makes it probable that the occurrence of occasional specimens of the dry phase of *sesamus* in January and February is a normal overlap.

Very careful and numerous records over a large number of years would be required to show that any change in the relative time limits of the two forms is taking place.

Owing to the kindness of Mr. S. L. Hinde, H. M. Sub-Commissioner, East African Protectorate, and Mrs. Hinde, I have received a most interesting series of the two forms from British East Africa, probably near the northern boundary of the range of the species. The numbers, captured in a short time on a limited area, are sufficient to enable us to judge of the relative proportions of the two forms, and we see that in May and the beginning of June the two occur mixed in about equal proportions, while in December and January the wet phase greatly predominates, although an occasional dry form appears, as it does in Mashonaland, early in January. I have included in the series two other specimens from near the northern part of the range of *P. sesamus*. The whole list is wonderfully similar to that from Mashonaland, and supports the view that Mr. Marshall's observations record the normal mode of replacement of the wet by the dry phase, although the former persists in large numbers much later in the north than it does in the south.

LOCALITY.	OBSERVER.	DATE.	FORM OF *Precis sesamus* IN HOPE COLLECTION.	CHARACTER OF THE SEASON AT WHICH CAPTURE WAS EFFECTED.
N. Kiknyu Country, 5000 ft.	H. J. Mackinder and C. B. Hausburg.	Aug. 1899.	1 *sesamus*, fresh.	The heart of the big dry season. Butterflies very scarce.
Near Mengo, Uganda.	Mrs. Leakey.	May 30, 1900.	1 *natalensis*, fresh.	
Machakos Road.	S. L. and H. Hinde.	May 22, 1900.	6 *natalensis*, mostly worn. 6 *sesamus*, fresh. The 12 insects captured in less than an hour on a patch of ground a few yards in extent.	The end of a very dry wet-season in an exceptionally dry year.
Machakos.	S. L. and H. Hinde.	June 6, 1900.	2 *natalensis*. 1 variety nearer to *natalensis*. 3 *sesamus*. 1 *natalensis*, is worn, all others fresh. The 6 insects captured together as above.	As above, only well into the dry season. Two or three days' heavy rain had intervened between this date and May 22.
Kitui.	S. L. and H. Hinde.	Dec. 11, 1900.	4 *natalensis*, mostly worn.	After the rains of the small wet season, and in the beginning of the small dry season.
		Jan. 2, 1901.	4 *natalensis*, mostly fresh. 1 *sesamus*, fresh.	Nearly in the middle of the small dry season.
		Jan. 8, 1901.	1 *natalensis*, little worn.	Nearly in the middle of the small dry season.
		Jan. 12, 1901.	1 *natalensis*, fresh.	Nearly in the middle of the small dry season.

The succession of the seasons is very different, in the region in which Mr. and Mrs. Hinde captured the butterflies, from that which obtains in Salisbury. The two forms of succession are shown in parallel columns below.

BRITISH EAST AFRICA (MACHAKOS, KITUI, ETC.).		MASHONALAND (SALISBURY, MAZOE, GADZIMA).	
Mid-October to Mid-December	Small wet season (about 17—18 inches).	Early November to Mid-April	Wet season, average rainfall of Salisbury about 35 inches.
Mid-December to Mid-March	Small dry season.		
Mid-March to end May	Big wet season (about 17—18 inches).	Mid-April to Early November	Dry season.
end May to Mid-October	Big dry season.		

It is to be observed that the rainfall of the small and the big wet seasons are about the same, and also that the country is not really dried up in the small dry season except in unusually dry years. The country is always dried up in the big dry season.

In spite of these great differences in the seasons, the succession of the phases is wonderfully alike in the two areas, as has been pointed out above. We must conclude that *sesamus* can produce two seasonal phases annually but not more, so that the small dry season of the north is no more effective in producing the dry phase than the simultaneous wet season of the south. The species is so constituted that it produces a dry phase for the big dry season and a wet phase for the rest of the year, some of the dry-phase individuals being produced some months before the normal change takes place, viz. at and just before the beginning of the chief dry season. The difference between the date at which this great change of seasons takes place in north and south is attended by a corresponding difference in the date at which the wet phase of *sesamus* gives place to the dry. Both lists are unfortunately wanting at the transition from the big dry season to the wet. There is indeed only a single record for the period between the beginning of June and the beginning of December. Speaking from memory, Mr. Marshall thinks that the break from *sesamus* to *natalensis*

at the beginning of the wet season is not sharp; indeed, he has a distinct recollection of seeing them flying together at that season fairly frequently. "I believe," he writes (1902), "that in some seasons one might take *sesamus* in every month of the year. Certainly at Gadzima, in 1895, the true winter broods of *sesamus* lasted right up to the end of December. In a dry spring, that is when the rains are late in starting, butterfly life appears to be less abundant and the emergence of the wet-season forms seems to be retarded. On such occasions an actual break without specimens might occur in such a comparatively unfavourable locality as Salisbury. But I believe that this would be an unusual occurrence, and even if it happened in one locality I doubt if it would necessarily take place everywhere at the same time; for example, in the moister parts of the low veldt the succession of the broods would probably continue unbroken. I am quite satisfied that there are at least two or three broods of *sesamus* during the winter months, that is if the condition of wild specimens can be taken as any criterion. Food is much less plentiful in the winter, but it is obtainable in quite sufficient quantities to keep the species going. The change of seasons from wet to dry is of rather a gradual character; the reverse change is more marked, but this depends a good deal upon the total rainfall of the preceding year. When this has been heavy, the ground retains a certain amount of moisture throughout the winter, so that when the frosts cease and the sun's heat increases in the spring, a large number of the earlier plants spring up and flower before a drop of rain has fallen. But after a succession of dry years this does not take place, and, with possibly a few exceptions, none of the plants come out in response to the heat, but require the rains to bring them out. In this latter case the change in conditions is very strongly marked, much more so than during a wet cycle."

The discussion of the possible nature of the environmental stimulus, if any, is better deferred until after the description and consideration of Mr. Marshall's experiments in the next section.

H. *The attempt to control the Phases of* P. sesamus *and* P. archesia *by the artificial application of Moisture and Heat to the earlier stages. Suggested lines of Experiment.*

All the experiments hitherto made by Mr. Marshall were directed towards the production of the wet *natalensis* and *pelasgis* phases in place of the dry *sesamus* and *archesia* respectively. The whole of the specimens produced were presented by Mr. Marshall to the Hope Collection, and all are tabulated below, together with a statement of the experimental conditions which were employed in each case. All experiments were made at Salisbury.

The following extracts from Mr. Marshall's letters refer to some of the experiments on *sesamus*:—

"*Salisbury, June* 5, 1898.—I kept two larvæ in a damp jar, but one did not attach itself properly when pupating, and the resulting pupa fell down when soft and was killed. The other larva produced a black pupa which emerged as the wet form [April 13, 1898, in the Table below], but this was rendered nugatory by the fact that one of the larvæ in normal conditions produced the same form, though from a gilded pupa [April 20, 1898, in the Table below]."

"*Salisbury, April* 25, 1899.—I have fourteen bred specimens of *P. sesamus* which I will send later [specimens in year 1899 in the Table below]; I tried some experiments with them, but the results are mostly negative. There are two interesting varieties, one with a red bar in the discoidal cell and another with the red spots much reduced."

NUMBER OF EXPERIMENT.	DATES OF EARLIER STAGES.	SURFACE ON WHICH LARVA SUSPENDED ITSELF.	COLOUR OF PUPA.	CONDITIONS OF HEAT AND MOISTURE.	DATE OF EMERGENCE.	PHASE OF *P. sesamus*.	SEX.	WEIGHT ON JUNE 30, 1902.
1	Larva suspended Feb. 19, pupated Feb. 21.	White paper.	Gilded.	Dry heat Feb. 21—28.	March 1, 1899.	1 *natalensis*.	♀	·07322 grammes.
2	Larva suspended Feb. 21, pupated Feb. 22.	Crimson paper.	Black.	Dry heat Feb. 22—March 1.	March 6, 1899.	1 *sesamus*.	♂	·08422 grammes.
3	Larva suspended Feb. 22, pupated Feb. 23.	White paper.	Gilded.	Dry heat Feb. 23—March 2.	March 6, 1899.	1 *sesamus*.	♀	·07807 grammes.
4	Larva suspended Feb. 24, pupated Feb. 24.	White paper.	Gilded.	Dry heat Feb. 24—March 2.	March 9, 1899.	1 *sesamus*.	♀	·10422 grammes.
5	Larva suspended Feb. 24, pupated Feb. 25.	White paper.	Gilded.	Dry heat Feb. 25—March 2.	March 10, 1899.	1 *sesamus* (with red bar in cell of fore-wing).	♀	·08522 grammes.
	Larva suspended Feb. 24, pupated Feb. 25.	White paper.	Gilded.	Dry heat Feb. 25—March 2.	March 10, 1899.	1 *sesamus*.	♀	Not weighed; mended specimen.
7	Larva suspended March 3, pupated March 4.	White paper.	Gilded.	Damp heat March 17, 7 p.m. to March 18, 2 p.m.	March 19, 1899.	1 *sesamus*.	♂	·07772 grammes.
8	Larva suspended March 9, pupated March 10.	White paper.	Gilded.	Damp heat March 17—21.	March 22, 1899.	1 *sesamus*.	♂	·05272 grammes.
9	Larva suspended March 11, pupated March 12.	Green stem in white box.	Gilded.	Damp heat March 17—23.	March 24, 1899.	1 *sesamus* (red spots much reduced; bright blue shade of ground-colour).	♀	·06972 grammes.
10	Pupated April 1.	—	—	Damp March 23.	April 13, 1898.	1 *natalensis* (*sesamus* dominant in nature in middle of March).	♀	·04647 grammes.
11	Egg laid March 6, hatched March 12, pupated April 7.	—	—	Damp March 30—April 5.	April 30, 1898.	1 *sesamus*.	♂	·07172 grammes.
12	Egg laid Feb. 27, hatched March 5, pupated March 31.	—	—	Normal.	April 15, 1898.	1 *sesamus*.	♂	·06447 grammes.
13	Egg laid Feb. 27, hatched March 5, pupated April 5.	—	—	Normal.	April 20, 1898.	1 *natalensis* (but somewhat dark variety).	♀	·06722 grammes.
14	Larva suspended Feb. 26, pupated Feb. 27.	Brown paper.	Black.	Normal.	March 13, 1899.	1 *sesamus* (dark with small red spots).	♂	·07847 grammes.
15	Larva suspended Feb. 27, pupated Feb. 28.	Brown paper.	Gilded.	Normal.	March 13, 1899.	1 *sesamus*.	♂	·07372 grammes.
16	Larva suspended Feb. 28, pupated March 1.	Brown paper.	Gilded.	Normal.	March 16, 1899.	1 *sesamus* (largest red spots of all these imagines).	♀	·10097 grammes.
17	Larva suspended Feb. 28, pupated March 1.	Brown paper.	Gilded.	Normal.	March 15, 1899.	1 *sesamus* (very dark with small red spots).	♂	·09097 grammes.
18	Larva suspended March 3, pupated March 4.	White paper.	Gilded.	Normal.	March 19, 1899.	1 *sesamus*.	♀	·09397 grammes.

The experiments on the power of adaptation of the pupal colours to their environment are very interesting, and prove that the susceptibility resembles that of the allied British species *Vanessa urticæ*. They also show that there is no essential difference between the colours of the pupæ of the two phases, but merely an adaptive response to environments which differ in colour at the two seasons, as suggested by Mr. Marshall (Ann. and Mag. Nat. Hist., July 1898, p. 33). It is clear, from the experiments, that if withered leaves of the usual winter yellow appeared, owing to exceptional circumstances, in the summer, larvæ suspended to them would produce gilded pupæ instead of the usual dark summer forms, and, *mutatis mutandis*, larvæ would produce dark pupæ upon dark leaves in the winter.

The highest form of procryptic defence, viz. the power of each individual to respond adaptively to any of its different normal environments, here exists in the helpless pupal stage, although the under-side of the wet phase of the imago can only be interpreted on the supposition that natural selection has developed a conspicuous appearance. Our own *Vanessidæ* however offer examples of the same kind of association in the different stages of a single life history. Thus the pupæ of *V. urticæ* and *V. io* have the same specialized power of concealment, while their gregarious black larvæ are excessively conspicuous and the imagines themselves by no means palatable to certain enemies of insects (see p. 442).

No special significance appears to attach to the varieties of the imagines produced in these experiments. The red bar in the cell of No. 5 is a common variety which indeed appears to be universal in the dry phase of the West African *P. octavia*, and red scales can be detected in this region in a large proportion of the individuals of *P. sesamus*. The red spots of No. 5 are not specially developed. The latter were largest in an individual exposed to normal conditions (No. 16), while Nos. 14 and 17, also exposed to normal conditions, were among the specimens with the smallest spots. The bright blue shade of the ground-colour of No. 9, exposed to damp heat, is well known in captured specimens from the most northern part of the range of the species as well as the south.

The specimens were weighed on an Oertling's balance, each pinned on a small cork foot which weighed ·06275 grammes on June 29, 1902, and ·00025 grammes more on

June 30. The weight of the No. 16 pin (D. F. Taylor's) was obtained by weighing three sets of ten similar pins. The weight of the first ten was ·7960 grammes, of the second and third ·7950 grammes. The average weight of a pin was therefore ·07953 grammes, and this number added to ·06275 was deducted from each of the specimens weighed on June 29 (see p. 456): added to ·063 it was deducted from the specimens of the experiments recorded above, and all others weighed on June 30 (see pp. 451, 456). On the latter date the cork foot was weighed at the beginning of work, in the middle, and at the end. On all three occasions it weighed ·063 grammes.

The consideration of the experiments on *Sesamus* is better deferred until after describing those upon *archesia*, although it is at once evident that no positive conclusions can be drawn as to the nature of the environmental stimulus. The negative character of the results obtained induced Mr. Marshall finally to form the opinion quoted below.

"*Salisbury, Feb.* 26, 1902.—I do quite agree with you now that in the case of *Precis* the evidence is sufficiently strong to show that climate has ceased to operate as the stimulus which calls forth the seasonal change. But I do not think that this view is applicable to other genera whose changes coincide closely with the changes in climate. The theoretical proposition I would suggest is that at its inception seasonal change was but slight and then due entirely to climatic action, such cases doubtless occurring at the present time. Any markedly useful variations of this kind would then be preserved and accentuated by natural selection, but climatic causes would still remain the controlling factor. Finally, as in *Precis*, the influence of natural selection would attain its maximum, and the seasonal changes would then take place solely as a result of this principle and irrespective of the influence of climate. It remains to be seen whether this can be proved by experiment."

On pp. 455 to 458 it will be seen that there are still hopes that the operation of some environmental stimulus may yet be discovered in the case of *Precis*.

The results obtained from the smaller series of experiments upon *P. archesia* are even more negative than those yielded by *P. sesamus*, as will be seen by a glance at the Table below, giving a complete account of all that has been as yet done.

DATES OF EARLIER STAGES.		CONDITIONS.	DATE OF EMERGENCE.	RESULT OF EXPERIMENT.
—		Normal.	April 20, 1899.	1 *archesia*.
Pupated March 28.		Normal.	April 14, 1899.	1 *archesia*.
Offspring of same parent *pelasgis*.	Egg laid March 22, hatched March 27, pupated April 24.	Normal.	May 7, 1899.	1 *pelasgis* } *archesia* had replaced *pelasgis* about beginning of April.
	Egg laid March 22, hatched March 28, pupated April 26.		May 14, 1899.	1 *pelasgis* }
Pupated April 14.		Damp heat April 14—22.	April 28, 1899.	1 *archesia*.
Recorded in Ann. Mag. Nat. Hist., November 1901, p. 400.	Pupated April 17.	Damp April 16—May 6.	May 8, 1901.	1 *archesia*.
	Pupated April 30.	Damp April 28—May 17.	May 21, 1901.	1 *archesia*.
	Pupated May 6.	Damp May 5—May 28.	May 30, 1901.	1 *archesia*, var. *staudingeri*.

Concerning the specimens which emerged on May 7 and 14, and April 28, 1899, Mr. Marshall wrote as follows:—

"*Salisbury, Aug.* 29, 1899.—The case of *pelasgis* and *archesia* was very puzzling, as the results were just the opposite of what one would expect—the forced pupa emerging as the dry-form *archesia*, and the normal ones as the wet-form *pelasgis*, though this latter has disappeared for some time, being replaced by *archesia*."

The negative results from these fairly-numerous experiments tempt us to believe that the change from *sesamus* to *natalensis* and *natalensis* to *sesamus* may be fixed in the constitution of the species, and may form an alternating series contemporaneous with the alternating seasons but not causally connected with them. Such a view is however rendered improbable, as Dr. Dixey has pointed out to me, because there would be nothing to prevent a gradual shifting and finally an entire want of parallelism between the two series. That, however, the change is essentially constitutional in the species and merely requires some external stimulus to set it going may be taken as certain. Furthermore, it is not necessary to suppose that a stimulus is required for *both* changes, the return to one of them, and presumably the more ancestral, may be in the nature of a rebound. The slight but distinct difference between the succession of the forms of *sesamus* in British East Africa and in Mashonaland also probably indicates a causal relation with the inorganic environment, and the same conclusion is supported by the fact that *artaxia* has been observed without its wet-season phase in a forest region (see pp. 422–3).

After Mr. Marshall's experiments it is difficult to believe that the application of heat or moisture or the two combined to the pupal stage can determine the production of *natalensis* or *pelasgis* in place of *sesamus* or *archesia*, respectively, at the period when the latter forms are becoming abundant in nature. It is possible that here we are merely witnessing the return to a more ancestral phase due to purely internal causes. The reverse experiment, viz. the application of cold, or dryness, or both combined, to pupæ of the earlier generations of *natalensis*, might produce more positive results and cause the appearance of *sesamus* at a time of the year when it is very rarely seen, although the occurrence of occasional individuals of *sesamus* in nature in the depth of the wet season seems to

be quite unrelated to dryness or cold (see pp. 443–8). But it would probably be necessary to apply artificial conditions to the larval stage. Indeed, the fact that the winter phases of certain species of *Precis* are so very much larger than the summer phases seems to require the conclusion that the change is pre-determined during or previously to the stage in which material is accumulated.

The differences in weight are well shown in captured individuals of two species in the following list: the method of procedure has been already described on pp. 452–3. It is seen that the dry phase always weighs more and sometimes over twice as much as the wet one.

SPECIES.	SEX.	LOCALITY.	DATE OF CAPTURE.	PHASE.	WEIGHT. FIRST 2 ON JUNE 29, REST ON JUNE 30, 1902.
Precis antilope.	♂	Salisbury.	March 2, 1898.	Wet.	·03422 grammes.
Precis antilope.	♀	Salisbury.	Feb. 27, 1898.	Wet.	·03747 grammes.
Precis antilope.	♀	Salisbury.	April 3, 1898.	Dry.	·07472 grammes.
Precis antilope.	♀	Salisbury.	March 9, 1898.	Dry.	·04947 grammes.
Precis artaxia.	♂	Umtali.	Dec. 27, 1900.	Wet.	·05597 grammes.
Precis artaxia.	♀	Umtali.	Dec. 30, 1900.	Dry.	·09672 grammes.
Precis artaxia.	♂	Umtali.	Dec. 30, 1900.	Dry.	·08447 grammes.
Precis artaxia.	♀	Gadzima, Umfuli R.	Dec. 29, 1895.	Wet.	·06622 grammes.
Precis artaxia.	♂	Gadzima, Umfuli R.	Dec. 30, 1895.	Wet.	·05422 grammes.
Precis artaxia.	♀	Gadzima, Umfuli R.	July 29, 1895.	Dry.	·06997 grammes.
Precis artaxia.	♀	Mazoe.	Dec. 28, 1894.	Wet.	·04522 grammes.
Precis artaxia (worn).	♀	Mazoe.	Oct. 23, 1894.	Dry.	·09547 grammes.

It may be argued that the results from captured specimens are untrustworthy because some females will have laid their eggs, some males will have paired, and others not. The five series of specimens of *sesamus* and *natalensis* bred by Mr. Marshall are not open to this objection and

are therefore of especial value. The weights of the eighteen bred specimens are given on p. 451, and it will be seen that the difference between the phases is very marked, although not nearly equal to that between the two forms of *artaxia*.

There is no escape from the conclusion that the larvæ of the dry phase of these species must be much larger than those of the wet, and must eat a great deal more food. This inevitable conclusion suggests that in experimenting on this most interesting of all known examples of seasonal change, it will be well to keep an open mind on all conceivable stimuli: on the abundance and character of the food-plant as well as the inorganic conditions of humidity and temperature, the latter of which has been proved by Dorfmeister, Weismann, Merrifield and Standfuss to be an effective stimulus in the case of certain Palæarctic seasonally dimorphic species. It is possible that the parched state of the food-plant towards the end of the dry season may be the stimulus which determines development in the direction of the smaller summer phase. The different sizes and weights render it nearly certain, as I have argued above, that the phase is predetermined in the larval stage. Now the larval stage of the first dry-season brood is passed in the wet season, and that of the first wet-season brood probably in the dry. We must look to some condition affecting one or both of these larval stages, or the eggs from which they arose, as the stimulus which sets in motion the organic processes resulting in a change of phase. Some colour of support is lent to the suggestion that the condition of the food-plant may afford the necessary stimulus by the fact that the wet phase of *P. artaxia* is unknown in certain forest regions, where it is probable that the food is not subject to the same alternation of condition as in more exposed stations. But forests would also act as moderating influences for extreme differences in temperature and humidity, and thus tend to prevent these from acting as stimuli for the species in question; for we know that some stimuli must be effective in producing such seasonal changes as occur in other forest species of *Precis* (see p. 423). Finally, quantity as contrasted with condition of food would be well worth trying. The unusually low weight of the imagines bred from the egg (Expts. 11, 12, and 13 on p. 451) was a probable result of difficulty in obtaining a constant supply of fresh

food in an entirely normal state, and it is noteworthy that one out of the three was *natalensis*. The extremely low weight of the ♀ *natalensis* in Expt. 10 also suggests some unfavourable condition in the larval state.

With the facts before us I do not see that any further suggestions can be made at the present moment; but I think the tables of weights clearly indicate the period at which the stimuli should be applied, while temperature, humidity, quantity or quality of food, or some combination of these, seem to exhaust all probable influences in the direction of a change of phase.

I. *The Bearing of the Seasonal Phases of* Precis *upon the Science of Insect Systematics.*

The results which have been described and illustrated in this section of the present memoir are so startling that they may well shake the confidence of naturalists in the whole fabric of insect systematics. If such forms as *natalensis* and *sesamus*, as *simia* and *antilope*, as *pelasgis* and *archesia*, are nothing but the generations of two alternating phases of a single species, approximately synchronized with the heat and cold or humidity and dryness of the alternating seasons, naturalists may feel driven to ask, "What becomes of the validity of specific distinctions?" Between the two phases of *Precis sesamus* there are extraordinary differences in colours, pattern, shape of wings, relation of upper- to under-side, nay, even in instinctive habits, including the choice of particular stations. This latter distinction between the phases is but the outward expression of some profound difference in the intimate structure of ganglionic centres and intercommunicating strands in the central nervous system. Important differences in venation are incidentally brought about by the great differences in the shape of the wing. The extreme rarity of intermediate varieties furthermore recalls the abrupt transitions which are so common, although very far from universal, between species of animals which are assumed to be distinct. Under the shock of Mr. Marshall's discovery that *sesamus* and *natalensis* are two forms of the same species, the systematist may well feel doubts about the foundations upon which his science has been erected. In these distracting circumstances a firm belief in natural selection will be found to

exercise a wonderfully calming and steadying influence. The structures which are adopted as the conventional criteria of specific distinction are of course modified by natural selection and brought into adjustment with new conditions of the struggle for existence as one species is gradually changed into another; but they are also capable of modification in one and the same species as it passes through various conditions during its life-history and in sexual and other dimorphism. The species frequently requires that the female sex should be more protected than the male, and hence we often witness a more perfectly cryptic appearance and habits in the female, and mimicry in the female alone. In many kinds of di-, tri- and polymorphism we see a species more perfectly protected at one and the same time by extending the area over which it must be sought by its enemies—in cryptic resemblance, earth and bark as well as leaves and shoots—in mimetic resemblance, Danaine or other distasteful models not of one species alone but two or more. In the di-, tri- or polymorphism of the social Hymenoptera and Neuroptera we see the specialization of the individual for the good of the community. In the extreme cases of seasonal dimorphism, exhibited by the genus *Precis*, there is a far less common modification of a species into two series of generations respectively adjusted to the conditions obtaining at two seasons of the year. But less marked cases of the same kind are probably not uncommon. There is however nothing revolutionary or subversive in any of these interesting facts. The conventional marks of specific distinction remain just as they were, convenient indications to the systematist, enabling him provisionally to separate groups of individuals into the assemblages we call species. When his work is done carefully subsequent breeding experiments will, we may be sure, confirm his conclusions in the majority of cases. But here and there startling exceptions will be found when it is to the advantage of a species to appear in two or more very different forms. In such cases the reason for the difference can generally be satisfactorily explained on the principles of natural selection; and when such an explanation is possible or even probable it is quite unnecessary to assume that the exceptions possess a numerical importance sufficient to shake the foundations of systematics.

Certain species are cryptic while others are aposematic

or pseudaposematic; certain stages in the life of an individual may be cryptic, others aposematic or pseudaposematic. There is nothing subversive in the thought that certain species exposed to different organic environments in two seasons of the year may appear as cryptic generations at one of these, aposematic or pseudaposematic at the other. The explanation is at any rate sufficiently probable to enable us to contemplate Mr. Marshall's wonderful discovery with equanimity and with an interest undisturbed by the thought that he has laid in ruins the whole edifice of insect systematics.

29. The Gregarious Instinct in Hybernation and Emigration of Insects. (E. B. P.)

The interesting observation that individuals of *Precis sesamus* are apt occasionally to congregate in large numbers as they go to roost, led me to reflect on the possible meaning of such an instinct. Mr. Marshall records other examples of the same kind "in species of *Euralia*, also in *Belenois*, *Herpænia criphia*, and *Teracolus eris*" (Ann. and Mag. Nat. Hist., *loc. cit.*, 1898, p. 34). It is possible that one interpretation does not explain all these cases, but I think it is probable that the observed instances of the congregating of *Precis* and *Euralia* are sporadic examples of an instinct which is associated with hybernation or, at any rate, a prolonged period of rest during a time of relatively excessive cold, heat, or dryness. Objection may be taken to this interpretation on the ground that large companies undergoing a prolonged rest ought to be well known in these species. It is possible however that the extreme conditions which render such a state desirable or even necessary for the species are not common, and, when they occur, do not conduce towards the active pursuit of natural history; furthermore, such prolonged rest would probably be passed through in some hidden recess which could only be found by accident.

Large numbers of naturalists for hundreds of years have been interested in the doings of *Vanessa io*, but, so far as I am aware, it is not generally known that this species may display a gregarious habit in hybernation.* My friend,

* Edward Newman recorded the occurrence of a company of more than forty *V. io* in a hollow oak (British Butterflies and Moths, London, N.D., p. 16), and the Rev. Joseph Greene disturbed three